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Why deer shed antlers¹

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Abstract

This paper discusses hypotheses explaining the shedding of antlers and horn-sheaths in deer and *Antilocapra* respectively. A number of earlier hypotheses pertaining to antler-shedding are reviewed critically; the views that antlers evolved to store excess minerals or hormones or shed excess heat are found wanting.

A theory explaining the shedding of hornlike organs must account for the origin of this

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phenomenon and its subsequent differentiation in different groups of deer and in *Antilocapra*. We agree that the KITCHEN-McCULLOUGH hypothesis explains the phylogenetic origin of horn-shedding in the Antilocapridae and point out that it explains the peculiar horn cores of the extinct merycodontids. In deer, antlershedding probably arose originally analogous to must in elephant or to differential coat colouring in the Indian black buck. Antlers were strictly associated with the rut state. The shedding of antlers is then related to female mimicry as a means for exhausted males to escape predation after the rut. An alternative to female mimicry by males is to segregate from females after the rut, a strategy adopted by highly evolved old-world deer. Antler shedding here is timed by the spring disbandment of males. The foregoing hypotheses explain a diversity of phenomena previously unexplained in the biology of old-world and new-world deer as well as *Antilocapra*.

Introduction

One of the mysteries of ungulate biology is why deer shed antlers annually. Among the hollow-horned ruminants, only the American pronghorn antelope has a distinct annual cycle of shedding and regrowing its horns. We are not concerned here with the proximal or physiological causes of antler or horn shedding. For those interested in these processes, we refer to Goss (1963, 1970) and O'GARA and MATSON (1975) for deer and pronghorns respectively. We are concerned with the ultimate or evolutionary causes of shedding. Why is it adaptive for deer and pronghorns to shed and regrow antlers and horns respectively?

In their reviews of antler functions. BRUHIN (1953) and BUBENIK (1966) listed three hypotheses proposed for the existence of antlers within which shedding and regrowth are a mandatory part. In this type of hypothesis it is the growing, but not the grown, hard antlers which fulfil some presumed annual function, so that the grown antler must be shed before a new growing set of antlers can fulfil the proposed role. The first hypothesis is that of KRIEG (1937 in BENINDE 1937), supported by BENINDE (1937) that antlers in their velvet state help to rid the body of excess minerals in the diet. The antlers are perceived as relief valves of a sort that free the body from an unneeded surplus. This hypothesis is shot down by the fact deer raid their skeletons for minerals in growing antlers (see BUBENIK 1966; Goss 1970).

The second hypothesis proposed by WILDHAGEN (in BUBENIK 1966) and STONEHOUSE (1968) sees the growing of antlers as a means of removing heat from the body during the spring and summer feeding flush. At that time, deer feed intensely, they grow fat, and the process of lipogenesis generates waste heat. Here it is surplus heat, not minerals, which are removed from the body. This hypothesis is untenable for many reasons, enumerated by GEIST (1968) and HENSHAW (1969).

The third hypothesis, proposed by RIES and by ZAPF (in Goss 1963 and BUBENIK 1966) sees antlers as a storehouse of sex hormones deposited in the antler during the period of growth and available after velvet shedding for the rut. This hypothesis founders on the fact that antlers are dead bone after the velvet is shed, without any vascularization that could carry hormones from the antlers to the body (Goss 1963; BUBENIK 1966).

None of these hypotheses are tenable. None predicts the time when deer should shed antlers, or explain the differences in the time of shedding between species.

HECK (1956), on the basis of his long experience with deer in zoological gardens, noted that antlers grow brittle and lose their effectiveness as organs of combat if not shed. To remain pliable effective weapons and defences, antlers clearly ought to be shed and regrown annually: This hypothesis is a case of special pleading. It does not explain why pronghorns ought to shed horn sheaths, fails to explain differences in shedding patterns between species, sexes and ages, and begs the question as to why harder and more durable antlers could not have been evolved.

KITCHEN (1974), referring to an idea of D. McCULLOUGH, explained shedding of horns in pronghorns as a mandatory consequence of the peculiar manner of horn growth in this species. In essence, if a pronghorn grows a set of horns, it cannot enlarge these subsequently. It can grow a larger horn only by casting the horn sheath of the old one, much as a deer cannot grow larger antlers without casting the old ones. In pronghorns the horn grows apically both upward and downward. If horn were added to the base of the old horn sheath, the old horn sheath would be lifted off and the growth centre would be sheared off. This is an ingenious special-case explanation and probably the correct one for the oldest phylogenetic reason for horn shedding in antilocaprids. Clearly, with apical growth, an annual enlargement of horns can only be achieved by horn shedding and growth of a larger horn sheath, as well as an annual increase in the horn core, as apparently practised by the merycodontids. This would be the first explanation offered for their peculiar morphology, as illustrated and discussed in BUBENIK (1966). The KITCHEN/McCULLOUGH hypothesis does not, however, explain why territorial bucks lose their horns before bachelor males or why horns are shed following the rut rather than many months later in the following spring. The foregoing illustrates an important point: there is some old phylogenetic reason why horns are shed and there are evolutionary reasons controlling the timing of the shedding.

At first glance, the following hypothesis appears a valid explanation of an ultimate evolutionary reason for antler shedding: it permits individuals to assume two different forms of resource exploitation, whereas the possession of permanent weapons limits the individual to one role only. This concept arose in discussing the evolutions of weapon systems (GEIST 1978a). Consider a small-bodied territorial ungulate. In forms such as these we find weapons maximizing surface damage, a correlate of resource defence. If its weapons are permanent, it may be fixed into year-round territorial defence. If it can shed its weapons, it can adopt an entirely different strategy of resource exploitation during the time in which new weapons are grown. This idea predicts that, if a small tropical deer should defend a territory all year round, it will not shed weapons annually. The genus *Mazama* may be such a deer (WAGNER 1960). It also predicts that in a family in which weapons cannot be shed, a given geographic area will be exploited by a multitude of species; in a family with weapon shedding, only a few, ecologically plastic and geographically widespread, species will be found. The evidence for ungulates is scanty but in line with these predictions (GEIST 1978a). However, as a hypothesis explaining antler shedding, it is untenable because it confuses cause and effect. Ecological plasticity can be considered a consequence of antler shedding, not its cause.

In a quest for the ultimate cause of antler shedding and regrowth, we must turn to the most primitive cervids, the tropical and subtropical old-world deer. Only for these, but not for the new-world equivalent, is there a useful paleontological record, so that we can identify old and young forms (THENIUS and HOFER 1960). Even the oldest form, as represented by *Muntiacus*, sheds antlers. In some, such as muntjacs from Ceylon, there is a weak synchrony of antler shedding (BARRETTE 1977); in others, such as muntjacs from Java, there appears to be none (HOOGWERF 1970). Breeding seasons were not found in the Ceylon muntjac, and BARRETTE (1977) emphasizes the lack of synchrony between antler growth and reproductive activity. Males with growing antlers, thus, remain sexually active, in contrast to northern deer such as red deer, for instance (LINCOLN 1972). In other deer from the subtropics and tropics, males experience annual rutting periods, but not all males may be in rut simultaneously, as in the chital (SCHALLER 1967; BARRETTE 1977) and, to a lesser extent, in the Timor deer (*Rusa timorensis*). It is not clear at present if, in these deer, males with growing antlers are incapable of breeding.

The phenomenon of antler shedding in the muntjac is, in principle, similar to must in the Indian elephant (*Elephas*). Although males remain sexually potent all year round, they may enter into a special rutting state, a state apparently conditional on a surplus of energy from maintenance (GEIST 1974a). We find a similar phenomenon, apparently, in the Indian black buck (*Antilope cervicapra*). Here males grow a dark coat, not so much upon reaching sexual maturity, but upon reaching relatively high dominance. Thereafter, males remain dark provided they remain dominant, while bachelor males may return to a reddish female-like summer coat. The degree to which males assume dark coat colour is thus a function of social position (CARY 1976). We therefore must note that changes in coat colour in the black buck, antler growth and shedding in primitive old-world deer and must in Indian elephants appear to be analogous phenomena. It appears that in such a system males may opt out of a highly competitive and expensive rutting state into one of reduced dominance, but without total loss of sexual potency. Even in a rather constant environment, some synchrony of mating may be selected for. Then males may be forced into a strategy of accumulating resources for strenuous mating activities and expending them during a short intense rut (see GEIST 1978a). Antler shedding, thus, probably originated in ancestral deer with a save/expend strategy in reproduction through selection against males which prolonged the rut state; when exhausted males shed weapons and symbols of maleness and dropped out of the rut. A secondary consequence of this was an enhanced ecological plasticity, as indicated here earlier and in GEIST (1978a).

Antler shedding and antipredator strategies

Whatever the ancient phylogenetic causes of antler and horn shedding in deer and antilocaprids may have been, in present forms we find a considerable diversity in the timing of shedding and patterns of hornlike organs. It is this which needs to be explained.

BROMLEY (1977) proposed the following hypothesis for horn shedding in pronghorns: horn shedding is a phenomenon which, first, reduces predation on males by female mimicry and, second, permits closely knit bisexual herds in winter. The males shed their male image by shedding horns. BROMLEY argued that males become thoroughly exhausted by the rutting activities and are, therefore, less capable of sustained running than females. After the rut, the males remain with females. Therefore, culling predators would soon associate the male image with greater ease of capture, and would concentrate on the males. Males incapable of shedding horns and assuming a female image would fall victim to predation relatively frequently. BROMLEY (1977) identified a series of attributes of pronghorn males with shed horn sheaths that at a distance would help them pass for females. Moreover, in the bisexual wintering herds, the reduction of agonistic signals on the males would permit males and females to forage without undue excitement caused by the males. Excitation is very costly in calories (see GEIST 1971a, 1974b). If males winter with the same females they breed, and therefore are able to increase the cost of maintenance for females who now carry their offspring, selection will favour males with neutral appearance while females are gestating.

BROMLEY's (1977) hypothesis explains why in pronghorns the horns ought to be shed right after the rut, and why territorial males should shed earlier than the non-territorial males (KITCHEN 1974). Clearly, the territorial males ought to be the most exhausted ones. We do not know, unfortunately, the amount of weight lost by pronghorn males during the rut; for other temperate- and cold-zone ungulates it is considerable (KNAUS and SCHRÖDER 1975; HEPTNER and NASIMOVIC 1967; BANNI-

KOV et al. 1961). BROMLEY's hypothesis hinges on the assumption that antelope avoid predation by congregating with conspecifics. That such is a mechanism of reducing predation is today an accepted theory (TREISMAN 1975). That the retention of 'maleness' mitigates against uniform spacing of individuals was demonstrated experimentally on chaffinches by MARLER (1956). This finding was developed further by MOYNIHAN (1968), who verified that aggregation is facilitated by similarity in body marking and form. HAMILTON and BARTH (1962) proposed that the casting of brilliant plumage and replacing it with a drab female plumage by sexually dimorphic males reduces predation during migration in large flocks. BROMLEY's hypothesis is predicated on the assumption that predators learn to select vulnerable sex-age classes and thus form search images, a concept that is verified (MUELLER 1971, 1975; WILSON 1975). What lacks verification is not the principle but its particular, namely, that wolves, coyotes and extinct Pleistocene predators distinguished male from female pronghorns on the basis of horn size.

If BROMLEY's (1977) hypothesis is valid, it ought to apply to other ungulates with similar life histories. In species in which there is a sexual dimorphism in antlers or horns, we expect males to shed hornlike organs if they mingle with females following the rut and form bisexual herds. We also expect that young males, not exhausted by the rut, will retain antlers even in bisexual herds. The alternative to antler shedding by males is to segregate from the females and form separate herds, go into hiding or search out small pieces of habitat far from the female home ranges where predators rarely visit.

Among deer, bisexual wintering herds are known from the roe deer (*Capreolus*), the white-tailed deer (*Odocoileus virginianus*), the mule deer (*O. hemionus*) and the caribou (*Rangifer*). In the roe deer, the rut is during July and August but antlers are not shed until October and November, when bisexual wintering and migratory herds may form (LETTOW-VORBECK and RIECK 1956; FLEROV 1952; KURT 1968). Once the antlers are cast, the males are not readily distinguished from the females. As the antlers grow again, the males may begin to drift away from the females, beginning in the case of old males as early as February (FLEROV 1952). In the white-tailed deer, the casting of antlers sets in right after the rut, in mid December, with the older males tending to cast first (BEHREND and McDOWELL 1967; SIEGLER 1968). They do form bisexual wintering groups after the rutting season in open landscapes such as the prairies of Alberta (KRAMER 1971). In a dense white-tailed deer population from Texas, BROWN (1974) found that males continued some association with females but also tended to form fraternal groups; a rather high percentage of males is seen as singles. This is confirmed by HIRTH (1977) for the same population, but for a woodland population he reported a disassociation of sexes following the rut. In Rocky Mountain mule deer, males go briefly into seclusion if exhausted by the rut or form small fraternal bands. They begin shedding antlers shortly thereafter and are seen frequently in female company. Most bucks are seen in bisexual groups in March and April when deer congregate on open areas with little snow (BOUCKHOUT 1972). Significantly, antler growth in mule deer does not begin until after this time, when countryside has lost much of its snow blanket; the deer disperse and the males begin moving to separate ranges. As long as males after the rutting season are likely to be with females, they show little antler development.

In caribou, males remain associated with females right after the rut but begin to drop out progressively to form small fraternal groups away from female ranges (PARKER 1972; BERGERUD 1974a and b). However, the segregation is not clean. A large fraction of the young bulls remain with females, and apparently so do a few of the old males as well. As expected, the big bulls drop antlers right after the rut. This is a prerequisite to HENSHAW's (1969) hypothesis that females retain antlers as a

means of warding off males at feeding craters during winter. Without the need for males to shed antlers following the rut, it would of course be adaptive for males to retain antlers and parasitize the labour of females which paw deep craters in the snow to reach covered forage.

The objection could be raised that, after antler shedding, caribou bulls can be distinguished from females by the absence of antlers. Although female barren-ground caribou do have antlers regularly, this is not the case for the primitive woodland caribou in which a high percentage of females may be without antlers (BANFIELD 1961; HEPTNER et al. 1961). The objection would, therefore, not be valid for the caribou form that probably gave rise to the barren-ground races. Woodland caribou show the same attributes of primitiveness found in other deer and bovid lineages (GEIST 1971b). Moreover, young caribou males, as expected, shed their antlers later than the females. They must, therefore, be the most serious competitors for the females. We find that females carry antlers of a size that matches those of 1.5–2.5-year old bulls. This, of course, supports HENSHAW's (1969) hypothesis of antler development and retention in female caribou, and it supports GEIST's (1974b) hypothesis explaining sexual dimorphism or monomorphism in ungulates. It is noteworthy that in caribou virtually no noticeable antler growth occurs in males until about May (KELSALL 1968), when bulls are largely segregated from cows as these are moving to the calving grounds with the bulls trailing far behind (PRUITT 1960; PARKER 1972).

An alternative to antler shedding and joining female groups on common or greatly overlapping wintering areas is to retain antlers, form fraternal groups after the rut and avoid females. The red deer and elk (*Cervus elaphus*) is a good example of this (see GEIST 1978b). The large males segregate into fraternal herds except for young stags not exhausted by the rut. These ought to be less susceptible to predation, and they do remain largely in female company. If old males ought to avoid females to avoid selective predation, then males ought to vacate traditional winter ranges once such ranges become utilized by females. Indeed, observations reported by FLOOK (1970) on colonizing elk confirm this. To the east of Banff National Park an area supporting large groups of bulls in winter was abandoned by males with increasing use of the area by cows.

It is postulated in a review of red deer and elk adaptive strategies by GEIST (1978b) that antler retention permits fraternal groups of bulls to live at a minimum cost of maintenance, so that the duration for which red deer and elk retain antlers is determined by the length of winter they experience. The longer the winter, the longer males ought to retain antlers. Since elk are a later descendent of the red deer group and have evolved in Siberia with its long winters, elk ought to retain antlers longer than red deer. This is found. Once antlers are shed, a stable dominance hierarchy can be maintained only with much overt aggression, and even then it need not form. Males may disperse. Antler drop causes severe social disruption, as LINCOLN (1972) found for red deer. Such is adaptive only when individuals can move without penalty; antler drop may thus serve to aid the breakup of the wintering herds of bulls and their subsequent dispersal to distant spring and summer ranges.

Bull moose (*Alces*) do not shed antlers immediately after the rut. The males form fraternal groups where moose densities permit it. However, antler drop coincides with the break-up of these fraternal groups and the dispersal of bulls just prior to the season of deep hard snow that tends to commence in January. Antlers are dropped beginning in mid- to late December (HEPTNER and NASIMOVIC 1967). Bulls interact agonistically with their front legs, weapons that can cause surface damage and therefore great pain. The high level of aggression in moose has been suggested to be a means of dispersing moose in winter (GEIST 1967; HOUSTON 1968, 1974; BERG and PHILLIPS 1972), for this would preclude the animals rapidly exhausting their

food supply. In late winter with its deep hard snow blanket moose may become virtually trapped. They feed less selectively and far more intensely on individual bushes than previously (HEPTNER and NASIMOVIC 1967); they suffer malnutrition; they are severely limited in their movements and make more frequent contacts with wolves (PETERSON and ALLEN 1974) while the size of their ranges is greatly reduced, the deeper the snow the greater the reduction (KNORRE in COADAY 1974, p. 431). This condition has been postulated to be the cause of the moose antipredator strategies and tactics, which in late winter are based in facing predators and fighting them (GEIST 1967, 1974b). Therefore, the casting of antlers in early winter, long after the rut, and the concomitant dispersion of bulls is seen as an adaptation to overwintering under conditions of deep hard snow when movements between different feeding areas by groups would be precluded.

So far we have examined deer. However, the conditions under which the pronghorn male casts antlers appear to be equally applicable to the saiga antelope (*Saiga tatarica*). During the rut, saiga males defend harems while bachelor males form herds of their own. However, after the rut, the harem-defending males do not drop their horns, but form fraternal bands away the other individuals, while the females and bachelor males unite to form bisexual groups (HEPTNER et al. 1961). That male saiga antelope suffer a great weight loss during the rutting season and are subject to greater mortality from predation is reported by BANNIKOV et al. (1961). For *Gazella subguterosa*, HEPTNER et al. (1961) report the same pattern as for *Saiga tatarica*. The males segregate from the females right after the rut in December, but join the large herds of females and juveniles about a month later, in January. It may be noteworthy to add that in mountain bovids, there is a postrut segregation of males from females, with the older males leaving first and younger males often staying behind. This is valid for sheep (*Ovis*) (GEIST 1971c) and mountain goat (*Oreamnos*) (GEIST 1965), as well chamois (*Rupicapra*) (KNAUS and SCHRÖDER 1975) and ibex (*Capra ibex*) (NIEVERGELT 1966). In these forms and old-world deer from cold climates, the males do not cast the symbols of maleness and segregate from females; in pronghorns and most new-world deer, the males join females but cast their symbols of maleness.

Antler and horn shedding, thus, appear to be old adaptations which have been altered in different species by different methods of avoiding predators. The casting and regrowth of antlers and horns in pronghorns is thus analogous to plumage changes in some birds, with predation apparently being the main driving force.

Zusammenfassung

Warum Hirsche Geweihe abwerfen

In dieser Arbeit werden Hypothesen dargelegt, die den Abwurf der Geweihe der Cerviden und des Gehörns des Gabelbocks (*Antilocapra*) erklären. Ältere Deutungen dieses Phänomens werden kritisch diskutiert. Die Vorstellungen, daß Geweihe der Mineralien- oder Hormonspeicherung dienen oder sich als Organe zur Abgabe überschüssiger Wärme entwickelten, sind nicht aufrechtzuerhalten. Wir stimmen mit der KITCHEN-McCOULLOUGH-Hypothese überein, die den stammesgeschichtlichen Ursprung des Hornabwurfs bei Antilocapriden erklärt. Gleichzeitig trägt diese Hypothese zum Verständnis der eigenartigen Hornzapfen bei fossilen Merycodonten bei. Bei Cerviden müssen sich Besitz und Abwurf der Geweihe ursprünglich analog dem „must“-Phänomen bei *Elephas* oder entsprechend der Entstehung des Farbwechsels bei männlichen Hirschziegentantilopen herausgebildet haben. Das heißt, Geweihe wurden nur während der Brunft behalten. Im Anschluß an die Brunft stellten sie einen Nachteil dar, denn sie kennzeichneten den erschöpften, für Raubtiere anfälligen Hirsch. In gemischten Herden würde eine Selektion gegen geweihttragende Männchen einsetzen, vor allem gegen völlig erschöpfte. Als Alternative können sich Hirsche nach der Brunft von Weibchen trennen. Diese Strategie haben offenbar höhere Altweltthirsche eingeschlagen: die Geweihe werden bei Auflösung der Hirschverbände im Frühjahr abgeworfen. Diese Vorstellungen tragen zum Verständnis der Biologie von Neu- und Altweltcerviden und Antilocapriden bei.

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